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THE EYE OF *BYBLIS SERRATA*.

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Byblis serrata is an Amphipod Crustacean, which belongs to the family *Gammaridæ*, but has totally different eyes from *Gammarus*. A pair of these eyes projects from either side of the cephalon and any one of them calls to mind the vertebrate eye, because it has a biconvex lens and a fluid-filled space with a retina below. A section through the chief axes of the eye of *Byblis* would first show a large lens, which has been secreted in concentric shells by a thickened layer of lentigen, Fig. 4, *l*. continuous on either side with the thinner hypodermis *h*, which is gorged with scarlet pigment that envelops the eye like a cornucopia, thus shutting out all the rays that might reach the retina without first passing through the lens. Under the lentigen is a humor space, *s*. Below and proximal to this space is a layer of columnar cells, *x*, which is continuous on either side with the hypodermis. This layer of cells has secreted a strong cuticula on its outer boundary, which borders on the space, and just proximal to this layer are the omatidia (which, of course, lack the corneal cuticula). The most distal element of an omatidium is a granular columnar body (cell product), *r*. Below and proximal to this body, the remainder of the omatidium with its refractive cone and retinula is practically identical with the omatidium of *Gammarus*, minus of course, the corneal cuticula, for in the retinula of both crustaceans there are five retinal cells with pigment and four rhabdomeres.

METHODS.

The material employed in studying the eye of *Byblis serrata* was obtained at Mr. Alexander Agassiz's laboratory, at Newport,

R. I., during the summer of 1893, by skimming the surface of Narragansett Bay with a tow-net at night. Various killing reagents were tried, but the majority of specimens used and those giving the best results were killed in Kleinenberg's picro-sulphuric acid. Sections were cut on a Minot-Zimmerman microtome and stained with Kleinenberg's hematoxylin diluted with two parts of 70 per cent alcohol, and then decolorized in acid alcohol for ten minutes. This work was done under the direction of Dr. E. L. Mark, of Harvard University.

Structure of the Eye.

Byblis serrata possesses two pairs of crater-like eyes. One pair is a little anterior to the other, and also somewhat nearer the sagittal plane of the animal. The axis of the anterior pair makes a very acute angle with the chief axis of the body, pointing forward and upward. The ventral pair of eyes points downward and backward. In the living animal both pairs of eyes have a bright red appearance, owing to the presence of a large amount of red pigment surrounding the lens.

The component parts of the eye are best seen in sections passing through the chief axis. Beneath the thickened cuticula which constitutes the single lens is the succession of cell layers and cell products, which collectively form a roughly spherical mass, connected at its deep end by nerve fibers with the optic ganglia. Unlike the eyes of most Crustacea, which are the type known as compound eyes, in which clusters of cells called omatidia, acting independently of one another, are provided each with its own proportion of modified cuticula, the eyes of *Byblis*, although composed of clusters of cells, in some ways comparable with omatidia, nevertheless have but a single lens, so that they have a superficial resemblance to the eyes of spiders and other arachnids.

After I had studied this new and peculiar type of eye in detail, Della Valle's paper* on the '*Gammaridæ* of the Gulf of Naples' appeared, containing a figure and description of this same type of eye. The amphipod studied by Della Valle was *Ampelisca*, a genus closely allied to *Byblis*, but the author had not been able to resolve the omatidium into its separate elements. In *Ampelisca*, as shown by Della Valle's figure, the rods and cones differ slightly in shape from those of *Byblis*. Further, there is no pigment in the hypodermis adjoining the lens. In the lentigen of *Ampelisca* the nuclei are proportionately much larger than in *Byblis*, and the

*A complete bibliography of the literature on the eyes of amphipods will be found at the end of Dr. G. H. Parker's masterly paper entitled 'The Compound Eyes in Crustaceans' (Bull. Mus. Comp. Zool., XXI, 1891). The only recent histological paper on the eyes of amphipods of the family *Gammaridæ* is in Antonio Della Valle's 'Gammarini del Golfo di Napoli' (Fauna und Flora des Golfes von Neapel, XX, pp. 108–112, Tav. 46, Figs. 4–6, 1893).

lens shows no stratification. But the great and important differences are that the eye of *Ampelisca* has no humor space, lacks the middle layer of the eye of *Byblis*, while the latter possesses pigment, middle layer, and fluid-filled space.

Details of Histological Elements of the Eye.

Lens.—The lens is about the same size in each of the four eyes. Its outline is almost exactly circular in a surface view, and the curvature of the superficial and deep surfaces is nearly the same, Fig. 4, *len.* The lens, which is only a modification of the cuticula, shows even more plainly than the latter its composition of successive layers, the markings being as is commonly the case in lenses which are strongly convex, more or less concentric.

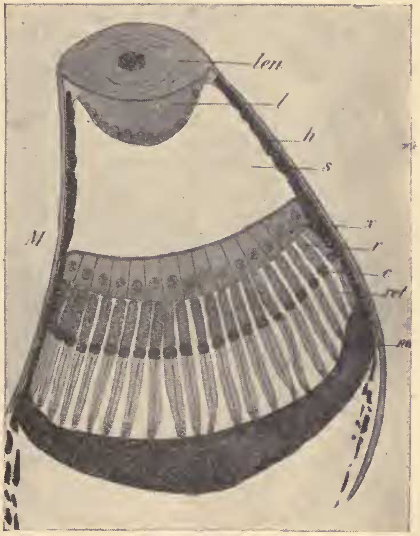

Fig. 4.—Diagrammatic section of right eye of posterior pair, slightly obliquely transverse to chief axis of body: *len*, lens; *l*, lentigen; *h*, hypodermis; *s*, space; *x*, middle layer of cells; *r*, rods; *c*, cones; *ret.*, retinulæ; *nu*, nuclear region of retina. × 350.

Lentigen. — There are three distinct layers beneath the lens, which in passing from the surface to the deeper portions I shall call respectively lentigen, middle layer, and retina. The lentigen consists of a single layer of elongated cells which radiate more or less regularly from the lens as a center, Fig. 4, *l.* They are of unequal lengths, those of the center being longest, and those nearer the margins of the lens successively shorter, so that the deep surface of the lentigen is usually hemispherical with a tendency to a conical form. The transition to the unmodified hypodermis is nevertheless quite abrupt. The nuclei of the lentigen cells are closely crowded in a single layer at the deep surface of the lentigen—often so closely that they are nearly twice as long as broad. They are granular and have distinct nuclear membranes. The hypodermis underlying the cuticula that surrounds the lens is filled with roughly spherical granules of pigment. The hypodermal cells form a single layer of epithelium, but the pigment obscures this structure to such an extent that it is almost impossible to make out the cell boundaries. In some sections, where this layer has been ruptured, nuclei are found which are supplied with a well defined membrane surrounding granular contents. So far as the nuclei are concerned, these pigmented hypodermal cells do not differ materially from the adjacent hypodermal cells that are lacking in pigment, Fig. 5, *h*.

Space.—Below the lentigen is a large space, which, in the living animal, is probably filled with fluid, for in none of my preparations is there any trace of structural elements. A conception of the form of this space may be obtained by taking a truncated cone of plastic modeler's clay and thrusting into the truncated surface a sphere, and supposing that there is a convexity corresponding to this hemispherical depression bulging out from the base of the cone. This modified truncated cone (the *space*) has its base formed by the slightly curving distal surface of the cells of the *middle layer*, Fig. 4, *x*, and the truncated surface is depressed by the inwardly projecting hemispherical lentigen, Fig. 4, *l*.

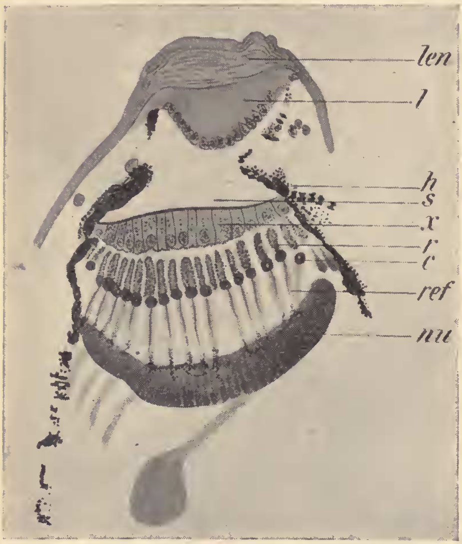

Fig. 5.—Section of left eye of the posterior and ventral pair, transverse to axis of body. Lens crinkled and hypodermis ruptured (abbreviations as in Fig. 4). × 300.

That this space is not artificially produced by shrinkage and consequent separation of the lentigen from the middle layer of cells is sufficiently evident from the constancy of its presence and form, but even more certainly from the fact that the deep surface of the lentigen and the outer surface of the middle layer cannot be imagined to have been in contact, for if they had been, such separation would have produced ragged ruptures and given conditions not shown in my series of slides.

Middle layer.—Below and proximal to the *space* is a single layer of columnar cells, Fig. 4, *x*. Like the lentigen, this layer is thickest in the middle, and diminishes very gradually and uniformly in thickness toward the margin. The contents of these cells are granular. The nuclei are situated in the proximal ends of the cells, and have coarsely granular contents and very faint, if any, nuclear membranes. The cells have remarkably well-defined cell walls. That this layer was not attached to and subsequently torn away from the lentigen by the microtome knife seems to be clearly shown by the fact that this middle layer has secreted on its distal surface bordering the space a thick cuticular-like structure.

Turning now to the parts of the eye lying proximal to the middle layer of cells, we notice that in all these deeper portions, which apparently correspond to the rods, cones, and retinulæ of Della Valle, there seem to be no nuclei, except those lying at the proximal or bottom part of the eye, which is clearly the nuclear region of the retina. The omatidia embrace at least the rods, cones, and retinulæ.

Rods.—The rods lie immediately beneath and proximal to the middle layer of cells, from which they are separated by a distinct line. The rods, Fig. 4, *r*, are somewhat more numerous than the cells in the middle layer. They are columnar, about as tall as the longest cells of the middle layer, but some of the marginal ones are shorter. The rods are coarsely granular. In oblique frontal sections through the chief axis of the eye there is an indication that each rod may possibly be made up of two parts.

Cones.—Beneath and proximal to each rod, and in close connection with it, is a crystalline cone, Fig. 4, *c*, which has a rounded cubical form and is highly refractive. Each cone is homogeneous except for a white space that usually occurs within its body. These spaces often have the appearance of more or less spheroidal cavities or vacuoles, but such vacuoles generally indicate the plane of separation between the two component parts of the crustacean cone. This apparent resolution of the cone into two parts seems to be indicated in cross-sections by two opposite sharp indentations of the outline.

Retinulæ.—Closely adhering to each cone is a bundle of five fusiform elements, Fig. 4, *ret.* The bundle at a deep level becomes resolved into its separate elements, and at a still deeper level closely packed nuclei of the retinula cells are found, Figs. 4 and 5, *nu.* These nuclei, which are completely filled with deeply stained granules, are flask-shaped. A cross-section through a fusiform bundle shows five granular retinula cells clustered about a highly refractive rhabdome composed of four rhabdomeres. At the place where the bundles are resolved a considerable amount of pigment is seen. In a cross section five μ thick each retinal cell contains about two grains of pigment. Nerve fibers have been traced from the optic ganglia to the region of the nuclear layer of the retina, but the exact connection with the retinal cells was not clearly seen.

Conclusions.

The eye of *Byblis serrata*, with its large lens, humor space, and complex omatidia, seems to be a compound eye built on the general plan of a simple ocellus, but also furnished with a space whose function may be like that of the vitreous humor space of the vertebrate eye. The true significance of this peculiar eye awaits the deft touch of the embryologist, who, in taking up this sense organ, will certainly enter a field where much is to be learned concerning the morphology of the arthropod eye.